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Genomic signatures of divergent selection are associated with social behaviour for spinner dolphin ecotypes

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Abstract

Understanding the genomic basis of adaptation is critical for understanding evolutionary processes and predicting how species will respond to environmental change. Spinner dolphins in the eastern tropical Pacific (ETP) present a unique system for studying adaptation. Within this large geographical region are four spinner dolphin ecotypes with weak neutral genetic divergence and no obvious barriers to gene flow, but strong spatial variation in morphology, behaviour and habitat. These ecotypes have large population sizes, which could reduce the effects of drift and facilitate selection. To identify genomic regions putatively under divergent selective pressures between ecotypes, we used genome scans with 8994 RADseq single nucleotide polymorphisms (SNPs) to identify population differentiation outliers and genotype–environment association outliers. Gene ontology enrichment analyses indicated that outlier SNPs from both types of analyses were associated with multiple genes involved in social behaviour and hippocampus development, including 15 genes associated with the human social disorder autism. Evidence for divergent selection on social behaviour is supported by previous evidence that these spinner dolphin ecotypes differ in mating systems and associated social behaviours. In particular, three of the ETP ecotypes probably have a polygynous mating system characterized by strong premating competition among males, whereas the fourth ecotype probably has a polygynandrous mating system characterized by strong postmating competition such as sperm competition. Our results provide evidence that selection for social behaviour may be an evolutionary force driving diversification of spinner dolphins in the ETP, potentially as a result of divergent sexual selection associated with different mating systems. Future studies should further investigate the potential adaptive role of the candidate genes identified here, and could probably find further signatures of selection using whole genome sequence data.

KEYWORDS
environmental association analysis, F_{ST} outlier tests, genome scan, genotype–environment association, mating system, *Stenella longirostris*

1 | INTRODUCTION

Understanding the genomic mechanisms underlying adaptation is an important step toward understanding evolutionary processes and can aid in conservation decision-making. Genomic mechanisms are often complex, but our ability to characterize these mechanisms has been propelled in recent years by the development of high-throughput sequencing technologies that enable "genome scan" approaches (Ahrens et al., 2018; McKinney et al., 2017; Rellstab et al., 2015). Thus far, studies using genome scans to investigate adaptative processes have been conducted more frequently for terrestrial than for marine species, probably due to the logistical complexity of collecting biological and environmental data from the ocean (Ahrens et al., 2018; Riginos et al., 2016). The dominant evolutionary pressures acting on marine populations are probably different from those acting on terrestrial populations, and probably operate on different spatial and temporal scales (Norris, 2000). For example, selection may be a particularly strong evolutionary force in the marine environment as a result of the very large population sizes for many marine species, because selection is highly effective in large populations due to the high numbers of new mutations that arise and the low impact of genetic drift (Allendorf et al., 2010; Peijnenburg & Goetze, 2013). Genome scan analyses conducted thus far in marine species have uncovered evidence for evolutionary mechanisms such as spatially varying selection for genes associated with bottom temperature, salinity and current velocity for sea cucumbers (Xuereb et al., 2018); divergent selection for genes associated with digestion across killer whale ecotypes that differ in prey type (Moura et al., 2014); and variation in selective pressures across depth gradients for deep-sea fish (Gaither et al., 2018).

Multiple statistical approaches have been developed to identify adaptive genomic divergence using genome scan data. Some approaches identify loci that are outliers for population differentiation, such as F_{ST} outlier tests (Francois et al., 2016) and principal components analysis (PCA) outlier tests (Luu et al., 2017). F_{ST} outlier tests identify loci with unusually high divergence between a priori defined populations, and thus these tests require multiple samples from each population, but can be used with samples from as few as two populations. PCA outlier tests identify loci that are strongly associated with population structure identified through PCA, and thus do not require prior knowledge of population structure or environmental data. In contrast, genotype–environment association (GEA) tests identify loci that are closely associated with environmental variables. These tests require environmental data for each sample, and require samples collected from across a wide range of environmental variation to achieve strong statistical power (Forester et al., 2018; Rellstab et al., 2015). Because GEA tests directly compare environmental variation with genetic variation, these tests can potentially provide greater insight into the ecological factors driving adaptation. Different outlier analyses may have different levels of power depending on a variety of factors including evolutionary history and sampling design, and therefore outliers that are consistently identified across methods may be the best candidates for further investigation (Lotterhos et al., 2017).

Here we use a combination of population differentiation and GEA outlier tests to investigate potential genomic adaptation for spinner dolphins (*Stenella longirostris*) across the eastern tropical Pacific (ETP). This vast region covers thousands of square kilometres and harbours four spinner dolphin ecotypes that have large population sizes and wide variation in morphology, habitat and behaviour, but are not strongly divergent at neutral genetic markers (Figure 1) (Andrews et al., 2013; Dizon et al., 1991; Galver, 2002; Leslie et al., 2019; Leslie & Morin, 2016). One of the most striking differences between ecotypes is the presence of different mating systems, with the whitebelly ecotype inferred to have a polygynandrous mating system, and the rest of the ecotypes (eastern, Tres Marias, Central American) a polygynous mating system (Perrin & Mesnick, 2003). Evidence for these different mating systems comes from strong differences between ecotypes in levels of sexual dimorphism and testis size variance, as well as high correlation between male-specific morphological traits and testis size (Perrin & Mesnick, 2003).

The presence of different mating systems in the ETP is thought to be driven by environmental variation across the ETP. Environmental variables that most strongly correlate with spinner dolphin ecotype distribution in the ETP include temperature, salinity and thermocline depth, and therefore these are among the variables that could drive divergent adaptive pressures. The thermocline has been proposed to act as a physical barrier to vertical movement of epipelagic species and a site of aggregation for vertically migrating mesopelagic species that are consumed by spinner dolphins (Ballance et al., 2006; Perrin et al., 1973). Since thermocline depth decreases eastward in the ETP, the effort required for prey capture by spinner dolphins is also thought to decrease eastward (Fiedler et al., 1998; Reilly & Fiedler, 1994). In addition, overall productivity of the marine habitat increases eastward in the ETP (Ballance et al., 1997; Reilly, 1990; Wyrtki, 1966). The higher availability of prey in the eastern portion of the ETP is thought to have driven the formation of a polygynous mating system in this region (Perrin & Mesnick, 2003), since high resource abundance enables males to expend greater energy competing for mates (Clutton-Brock, 1989; Emlen & Oring, 1977).

We used genotyping-by-sequencing (GBS; Elshire et al., 2011) to generate sequence data from thousands of loci across the genome for the four ETP spinner dolphin ecotypes, and used these data to test hypotheses about the role of natural selection in driving phenotypic differences among ecotypes. GBS is one approach within a family of restriction site-associated DNA sequencing (RADseq) methods that sequence regions adjacent to restriction cut sites, which are distributed relatively randomly across the genome (Andrews et al., 2016). Although RADseq approaches provide information regarding a subset of the genome rather than the whole genome, these approaches have been successfully used to identify adaptive genomic variation in many study systems (reviewed in Catchen et al., 2017; McKinney et al., 2017). We included samples collected from across the environmental gradient of the ETP, allowing us to use both population differentiation outlier tests and GEA outlier tests. Given the

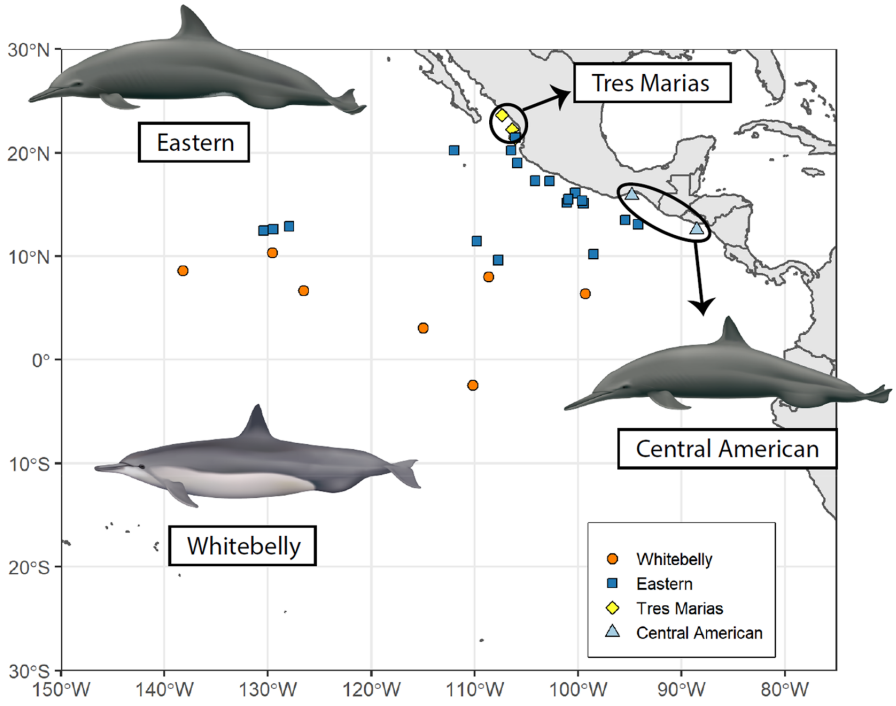

FIGURE 1 Sample collection sites for spinner dolphin (*Stenella longirostris*) ecotypes. Illustrations show the morphological differences between ecotypes (illustrations by Uko Gorter; used with permission) [Colour figure can be viewed at wileyonlinelibrary.com]

phenotypic and ecological divergence of spinner dolphin ecotypes within the ETP, along with their large population sizes, which should facilitate strong selection, we predicted that adaptive genomic variation was present. We expected these analyses to have strong power to detect adaptive genetic variation against the background of weak neutral population genetic structure across the ETP.

2 | METHODS

2.1 | Study system

Four spinner dolphin ecotypes have been described in the ETP, and are divided into three recognized subspecies (Committee on Taxonomy, 2019; Gerrodette & Forcada, 2005; Wade & Gerrodette, 1993). Within the ETP, the most phenotypically distinct ecotype is the whitebelly, a regional population of the globally distributed Gray's spinner subspecies (*S. l. longirostris*), which occurs in pelagic waters in the western ETP (Figure 1). This ecotype has a striped coloration pattern, whereas the other ecotypes are uniform in colour (Perrin, 1990). The whitebelly also differs from other ecotypes in body size, skull size, sexual dimorphism in body shape and dorsal fin shape, and life history characteristics including breeding season, ovulation and pregnancy rates, age at maturity, and testis size (Barlow, 1984; Perrin, 1990; Perrin & Henderson, 1984; Perrin & Mesnick, 2003). As described above, morphological evidence also points to the whitebelly having a polygynandrous mating system, and the other ETP ecotypes having a polygynous mating system (Perrin & Mesnick, 2003).

East of the whitebelly distribution occurs another pelagic ETP ecotype called the eastern ecotype (*S. l. orientalis*), and the geographical region between these two ecotypes harbours individuals exhibiting a morphological continuum between the two ecotypes. Further east in the ETP are the Tres Marias (*S. l. orientalis*) and Central American (*S. l. centroamericana*) ecotypes, which occur along the coast of Mexico and Central America. The Central American ecotype has a different skull shape than pelagic ecotypes, which suggests it feeds on larger prey (Perrin, 1972). Coastal ecotypes also differ from pelagic ecotypes in body size, schooling behaviour and calving seasonality, and the two coastal ecotypes differ from each other in body size (Chivers et al., 2019; Perryman & Westlake, 1998). Spinner dolphin population abundances in the ETP are estimated to have been reduced by about two-thirds due to bycatch in the tuna purse-seine fisheries of the 1960s and 1970s (Wade et al., 2007). However, post-depletion population sizes remain relatively large; post-depletion population census size estimates are available for the whitebelly ecotype (N > 1,000,000) and eastern ecotype (N = 450,000) (Gerrodette & Forcada, 2005; Wade & Gerrodette, 1993).

2.2 | Sample collection and genotyping

Generation of GBS data from tissue samples collected from 72 spinner dolphins from all four ETP ecotypes was previously described (Leslie & Morin, 2016). Tissue samples were collected between 1981 and 2006 and consisted of skin from field biopsy darting (Central American, Tres Marias and eastern ecotypes), or soft tissue from individuals that were bycatch in the tuna purse-seine fishery (eastern and whitebelly ecotypes) (Table 1; Table S1). As described in Leslie and Morin (2016), the ecotype associated with each biopsy sample was determined based on the external morphology of the majority

TABLE 1 Sample sizes for each spinner dolphin ecotype and diversity statistics for 8013 unlinked SNPs

		Sex					
	Total	Females	Males	Unknown	Number of pods	Years	H_E (95% conf.)
Whitebelly	13	7	6	0	8	1981–2001	0.104 (0.076–0.132)
Eastern	34	16	17	1	20	1984–2006	0.119 (0.100–0.139)
Tres Marias	12	6	6	0	2	2003	0.120 (0.087–0.154)
Central American	8	5	2	1	2	1998–2003	0.121 (0.079–0.164)
Total	67	34	31	2	32		

Note: H_E = expected heterozygosity (also known as gene diversity). 95% conf. = 95% confidence interval.

of the dolphins in the pod. For many of the fishery bycatch samples, detailed morphological data were available including colour pattern, dorsal fin shape and body length. These data had been used to assign a morphological code to each specimen; this code ranged from three to 10, with three representing morphology most typical of the eastern ecotype, and 10 representing morphology most typical of the whitebelly ecotype (Perrin et al., 1991). In addition, sex information had been collected either through direct observation of animals killed as fisheries bycatch, or via molecular methods for samples from free-ranging animals (Morin et al., 2005).

As described in Leslie and Morin. (2016), library preparation for the 72 samples followed the protocol of Elshire et al., (2011), using the restriction enzyme *Pst*I (CTGCAG), and duplicate libraries were prepared for two of the samples. All libraries were sequenced on an Illumina HiSeq 2000/2500 using 100-bp single-end sequencing. For the present study, three samples were removed from subsequent analyses due to low numbers of sequence reads (<600,000 reads). For the remaining samples, process_radtags in STACKS version 1.44 (Catchen et al., 2013) was used to remove reads with uncalled bases or with average phred scores <10 (90% probability of being correct) across a sliding window, and CUTADAPT version 1.17 (Martin, 2011) was used to remove 3′ Illumina adapters. Sequence reads were then aligned to the bottlenose dolphin genome (*Tursiops truncatus*, "Tur_tru_Illumina_hap_v1," GenBank assembly accession GCA_003314715.1) using BOWTIE2 version 2.1.0 (Langmead & Salzberg, 2012), using parameters --sensitive and --end-to-end. This genome assembly was chosen because it has the highest scaffold N50 of the three bottlenose dolphin genome assemblies currently available. After alignment, sam files were merged using SAMTOOLS version 1.9 (Li et al., 2009) for the two individual spinner dolphins that were intentionally sequenced in duplicate. Identification and genotyping of single nucleotide polymorphisms (SNPs) and indels were conducted with GATK version 3.5 (DePristo et al., 2011; McKenna et al., 2010) using per-sample variant calling with HAPLOTYPECALLER, followed by joint genotyping with GENOTYPEGVCF. VCFTOOLS 0.1.14 (Danecek et al., 2011) was used to remove indels, and to remove SNPs with genotype quality <15, with more than 5% missing data across all samples, with low mean depth (<8), with high mean depth (greater than the mean depth across all SNPs plus 1.5 times the standard deviation), or with minor allele frequency (MAF) <0.01. For genome scan outlier analyses, we implemented a more conservative MAF filter (MAF <0.05) to minimize the rate of false positives.

2.3 | Linkage decay

Patterns of linkage disequilibrium (LD) decay for each ecotype were visualized by plotting the squared allele count correlation (r^2) between all pairs of SNPs, except pairs more than 20 SNPs or 2 Mb apart, calculated using PLINK version 1.90 (Purcell et al., 2007). The results of these analyses were then used to evaluate the maximum distance over which SNPs are linked based on the distance at which r^2 reaches background levels. A "thinned" set of unlinked SNPs was generated that contained no SNP pairs separated by less than this distance using VCFTOOLS. This set of SNPs was used for all subsequent analyses except genome scan outlier tests.

2.4 | Relatedness analysis

To determine whether any duplicate samples or highly related individuals were present in our data set, we estimated relatedness (r) between each pair of individuals using COANCESTRY version 1.0.1.8 (Wang, 2011), which estimates seven relatedness estimators (Li et al., 1993; Lynch, 1988; Lynch & Ritland, 1999; Milligan, 2003; Queller & Goodnight, 1989; Ritland, 1996; Wang, 2002, 2007). We removed one of each pair of duplicates (r = 1) or highly related individuals (r > .25, indicating relationships equal to or closer than a half-sibling pair, grandparent–grandchild or aunt/uncle–nephew/niece) from all subsequent analyses.

2.5 | Population structure and diversity

To investigate diversity across ecotypes, we used ARLEQUIN version 3.5.2.2 (Excoffier et al., 2005) to estimate expected heterozygosity (H_E, also called gene diversity, Nei, 1987). We investigated population structure by estimating pairwise F_{ST} between each pair of ecotypes using ARLEQUIN, testing significance with 10,000 permutations. We also investigated population structure by conducting PCA

and sparse non-negative matrix factorization algorithms (sNMF) ancestry coefficient estimation using LEA version 2.4.0 (Frichot & Francois, 2015) in R version 3.5.1 (R_Core_Team, 2018). For sNMF analysis, we ran five iterations each for values of *K* ranging from one to five.

2.6 | Genome scan outlier tests

For GEA analysis, environmental parameters for each sample site were based on monthly means in 0.25 degree squares, from a composite of six ocean re-analysis data sets (Fiedler et al., 2017). Environmental parameters included sea surface temperature (sst), surface salinity, chlorophyll concentration (chl), mixed layer depth (mld), thermocline depth (td) and two measures of vertical temperature stratification: thermocline strength (ts) and standard deviation of temperature from 0 to 300 m (sdt) (Table S1). Data values for sample sites were spline-interpolated from the year–month composites as described in Fiedler et al., (2017). We tested for correlation between environmental variables using PSYCH (Revelle, 2018) in R and removed one of every pair of variables correlated with $|r| > .7$.

To identify SNPs associated with environmental variables, we used redundancy analysis (RDA). RDA is a multivariate, constrained ordination technique which analyses multiple loci and multiple environmental predictors simultaneously. This method uses multiple regression with all loci and all environmental variables to generate fitted genetic values, and then performs PCA with the fitted values. Loci with high loading values on the constrained ordination axes are identified as outliers. In simulations, RDA was found to be more powerful than univariate techniques for detecting weak, multilocus selection (Forester et al., 2018). In addition, these simulations found RDA to be robust to the presence of population structure, performing particularly well in isolation by distance scenarios, without correcting for population structure (Forester et al., 2018).

RDA was conducted with VEGAN 2.5-3 (Oksanen et al., 2018) in R, following the protocol described in Forester et al., (2018). Missing genotypes were imputed by replacement with the most common genotype at each SNP. Multicollinearity of variables was evaluated by calculating variance inflation factors. Constrained axes were considered significant if $p < .01$, and a SNP was considered an outlier if its loading was greater than three standard deviations from the mean on a significant constrained axis. To investigate the environmental variables most closely associated with outlier SNPs, Pearson correlation was calculated for each outlier SNP with each environmental variable. We also calculated the loadings of each individual dolphin sample on the RDA axes to evaluate the association of individual multilocus genotypes (rather than individual SNPs) with environmental variables.

We identified global F_{ST} outlier SNPs across ecotypes using two approaches: FDIST (Beaumont & Nichols, 1996) implemented in ARLEQUIN, and OUTFLANK version 0.2 (Whitlock & Lotterhos, 2015). FDIST uses a coalescent approach to estimate the distribution of F_{ST} values as a function of heterozygosity for neutral SNPs, and OUTFLANK uses a likelihood approach to estimate the distribution of F_{ST} values for neutral SNPs. We also used PCADAPT version 4.1.0 (Luu et al., 2017) to identify population structure outliers, using $K = 1$ principal component based on results of PCA (described further below); PCADAPT identifies SNPs that are outliers with respect to population structure ascertained through PCA. To account for multiple testing, we controlled the false discovery rate for OUTFLANK and PCADAPT, and used a Bonferroni correction for FDIST because the distribution of FDIST *p* values does not fit the expectation of false discovery correction. After identifying outliers for each of these F_{ST} outlier tests, we then used a Venn diagram to evaluate the consistency of outlier SNPs identified across each of these tests and the GEA method.

We then investigated population structure driven by putative adaptive SNPs by conducting PCA in LEA using (i) outlier SNPs, with a separate PCA for SNPs from each type of outlier analysis; (ii) outlier SNPs, with one PCA for the combined set of divergent selection outliers from all analyses (excluding balancing selection outliers, which would be expected to erode signatures of divergent adaption); and (iii) only nonoutlier SNPs, i.e., "neutral" SNPs that were not identified as outliers by any method. We also investigated the influence of outliers on F_{ST} values by conducting F_{ST} analyses in ARLEQUIN using (i) only divergent F_{ST} outlier SNPs, i.e., SNPs identified as selection outliers by FDIST or OUTFLANK; and (ii) only nonoutlier SNPs, i.e., neutral SNPs that were not identified as outliers by any analysis. For neutral SNP analyses, we first removed the outlier SNPs from the data set, and then "thinned" the data set as described above to create a set of unlinked nonoutlier SNPs.

2.7 | Gene ontology for outlier SNPs

To identify genes associated with outlier SNPs ("outlier-associated genes"), we used the genome annotations from the ENSEMBL *T. truncatus* ("turTru1," ENSEMBL version 95) genome, because the genome to which we aligned the RADseq loci is not currently annotated. To identify the positions of our SNPs in the turTru1 genome, we extracted 2000-bp regions around each SNP from our RADseq alignments using BEDTOOLS version 2.26.0 (Quinlan & Hall, 2010), and aligned these regions to the ENSEMBL turTru1 genome using BLASTN (NCBI BLAST+ version 2.7.1; Camacho et al., 2009). We accepted alignments with a maximum e-value of 10^{-20}, and then chose the best hit containing the SNP for each region. Only regions that matched over 1000 bp with at least 95% identity were retained; 91.0% of regions met these criteria. We used two gene ontology (GO) enrichment approaches to test whether genes associated with outlier SNPs were enriched for biological processes. For both approaches, we defined "outlier-associated genes" as those within 0.1 Mb of each outlier SNP; we chose this window based on results from the linkage decay analysis described above. The two GO enrichment approaches differed in the background gene list against which the outlier-associated genes

TABLE 2 Pairwise F_{ST} values (bottom of matrix) and p values (top of matrix) across ecotypes calculated using 8013 unlinked SNPs

	Whitebelly	Eastern	Tres Marias	Central American
Whitebelly		0.00050	<0.00001	<0.00001
Eastern	0.0029		0.00020	<0.00001
Tres Marias	0.0099	0.0026		0.00010
Central American	0.0104	0.0051	0.0058	

Note: Mean F_{ST} values per ecotype are as follows: Whitebelly: 0.0077; Central American: 0.0071; Tres Marias: 0.0061; Eastern: 0.0035.

were compared: the background list for the first approach comprised all genes within 0.1 Mb of the full set of SNPs in our data set, and the background list for the second approach comprised all genes in the turTru1 genome. The first approach has the advantage of taking into account potential sampling effects for the SNPs in our study, whereas the second approach provides greater statistical power to test for enrichment, while assuming that the SNPs in our data set are a representative sample of the genome. The first approach was conducted using GOWINDA version 1.12 (Kofler & Schlotterer, 2012) in gene mode, only testing GO terms with at least three genes (--min-genes 3) and performing 100,000 simulations (--simulations 100,000). The second approach was conducted with GORILLA (Eden et al., 2009), using default parameters for unranked lists of target and background genes. All annotation information was obtained from the ENSEMBL database via the BIOMART (biomart.org; Haider et al., 2009) interface. Both approaches generated p-values and false discovery rates (FDRs) for enrichment of biological processes.

3 | RESULTS

After removing samples with low numbers of sequence reads, one sample from a highly related pair and one unexpected duplicate sample (identified through relatedness analyses, as described below), our sample sizes for each ecotype were 13 whitebelly, 34 eastern, 12 Tres Marias and eight Central American (Table 1, Figure 1). The number of sequence reads ranged from 616,219 to 4,793,204 (mean = 2,227,120) across samples prior to filtering. The number of SNPs after filtering using MAF < 0.01 was 24,336, with mean read depth of 27.5 and mean missing data of 1.87%. For the genome scan analyses, the number of SNPs after filtering with the more conservative MAF filter (MAF < 0.05) was 8994, with mean read depth of 27.8 and mean missing data of 2.03%. The levels of missing data were similar across each of the filtered SNP sets; all except two individual samples had <10% missing data, and the highest level of missing data for any individual was 23%.

3.1 | Linkage decay

Linkage decay plots were created using the SNPs filtered for MAF < 0.01 and indicated linkage decreases rapidly until about 0.1 Mb and then stabilizes with mean r^2 close to zero (Figure S1). Based on these results, we generated a subset of unlinked SNPs by "thinning" the markers so that no two SNPs were within 0.1 Mb of each other. These SNPs were used for all subsequent analyses except genome scans. The number of SNPs after thinning was 8013.

3.2 | Relatedness analysis

Results of relatedness analyses were similar across all seven estimators; here we report results for the triad likelihood estimator (Wang, 2007). All except two pairwise relatedness estimates were <0.05, indicating that most individuals were not closely related (Figure S2). However, we identified one pair of samples with relatedness close to 1.0 (r = .999), indicating these two samples probably originated from the same individual dolphin (Figure S2). These two samples were collected from the same pod on the same day using field darting, and both samples were males from the Central American ecotype. We removed the sample with the lowest number of sequence reads from this pair for subsequent analyses. Another pair of samples exhibited substantially higher relatedness values than all other pairwise comparisons (r = .379) (Figure S2). Both of these samples were collected as fishery bycatch from the same pod, and both were from the eastern ecotype. Because these dolphins were fishery bycatch, detailed morphological data were available and indicated the two dolphins were morphologically similar (morphological code = 4 for both); one was male and the other female. Because all subsequent analyses in the present study assume sampled individuals are unrelated, we removed the sample with the lowest number of sequence reads from this pair for subsequent analyses.

3.3 | Population structure and diversity

When all 8013 unlinked SNPs were used, pairwise F_{ST} values were all significant (p < .001) and ranged from 0.0026 to 0.0104, with mean F_{ST} highest for the whitebelly (0.0077) and lowest for the eastern ecotype (0.0035) (Table 2). Genetic diversity was similar across ecotypes, with H_E ranging from 0.104 to 0.121 (Table 1). The first two axes of the PCA accounted for 4.01% of the variance (Figure 2a). Most putative population clusters overlapped, with the exception of the whitebelly, which clustered more separately (Figure 2a). Using the same data set, the sNMF minimal

cross-entropy results indicated $K = 1$ was the best fit (Figure S3a). Visual inspection of the ancestry assignment plots confirmed that this analysis discerned little divergence between ecotypes, although the whitebelly showed some evidence for clustering separately (Figure S3b).

3.4 | Genome scan outlier tests

Thermocline depth was strongly correlated with mixed layer depth ($r = .74$) and standard deviation of temperature ($r = .73$) (Figure S4). Therefore, we removed thermocline depth from the RDA to eliminate correlated variables. The first RDA axis was significant ($p = .001$) and was strongly correlated with sea surface temperature and mixed layer depth (Figure 3a). None of the remaining RDA axes were significant ($p > .698$). Variance inflation factors were all less than 10, indicating low multicollinearity among environmental variables. Twenty-two outlier SNPs were identified on the first RDA axis (Figure 3a; Table S2). Of these, 11 were most strongly correlated with sea surface temperature, nine with mixed layer depth and two with salinity. However, many of these SNPs had high correlations with more than one environmental variable, indicating these SNPs

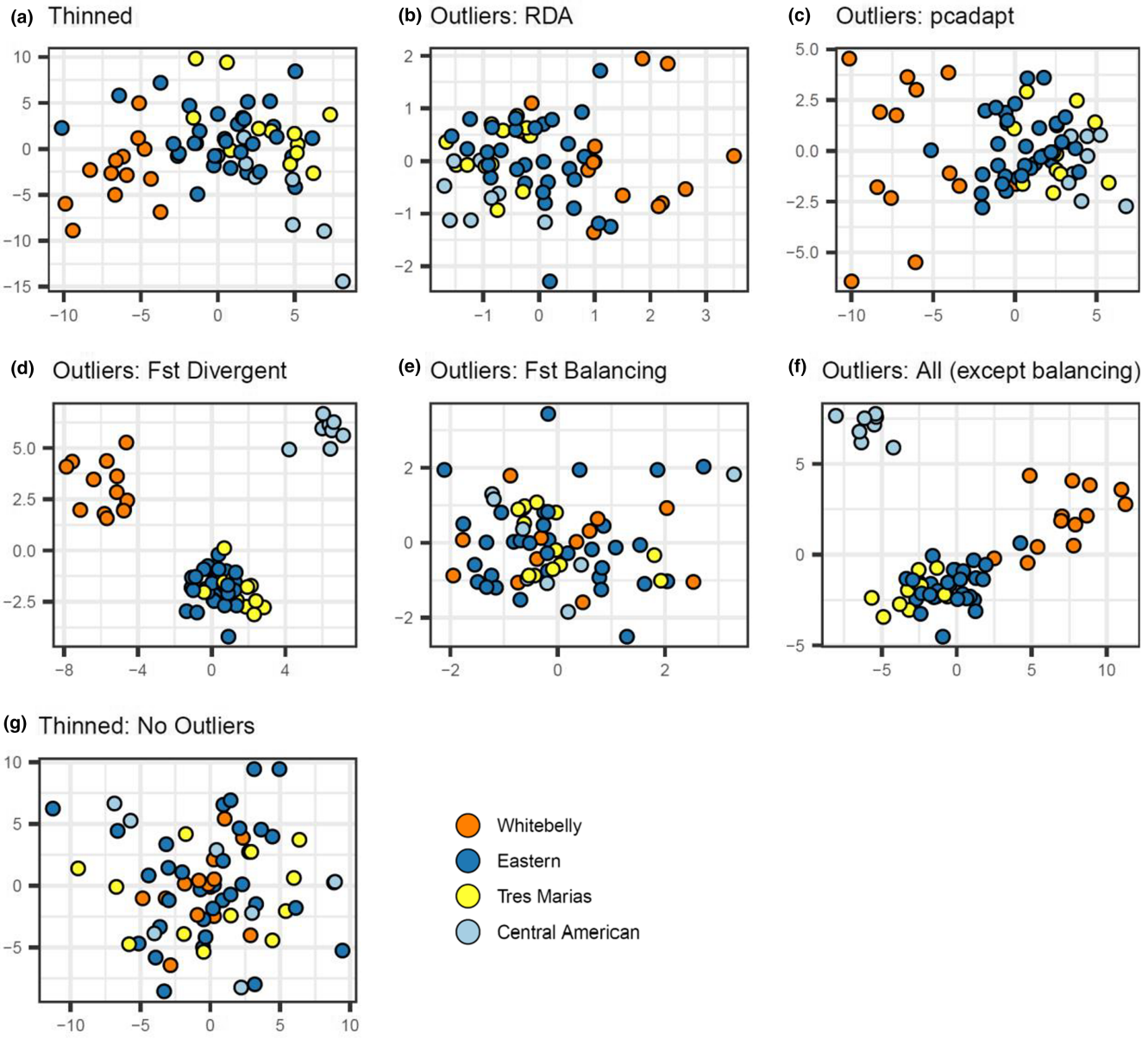

FIGURE 2 Principal components analysis (PCA) for spinner dolphin ecotypes using (a) 8013 unlinked SNPs, with 4.01% of the genetic variance explained by the first two axes, (b) 22 SNPs that were RDA outliers (32.6% of variance explained), (c) 537 SNPs that were PCADAPT outliers (13.2% of variance explained), (d) 645 SNPs that were global F_{ST} outliers for divergent selection in FDIST and OUTFLANK analyses (11.8% of variance explained), (e) 108 SNPs that were global F_{ST} outliers for balancing selection in FDIST analyses (10.8% of variance explained), (f) 990 SNPs that were outliers for any test, except outliers for balancing selection (10.8% of variance explained), and (g) 7863 unlinked SNPs that were not outliers for any test (3.88% of variance explained) [Colour figure can be viewed at wileyonlinelibrary.com]

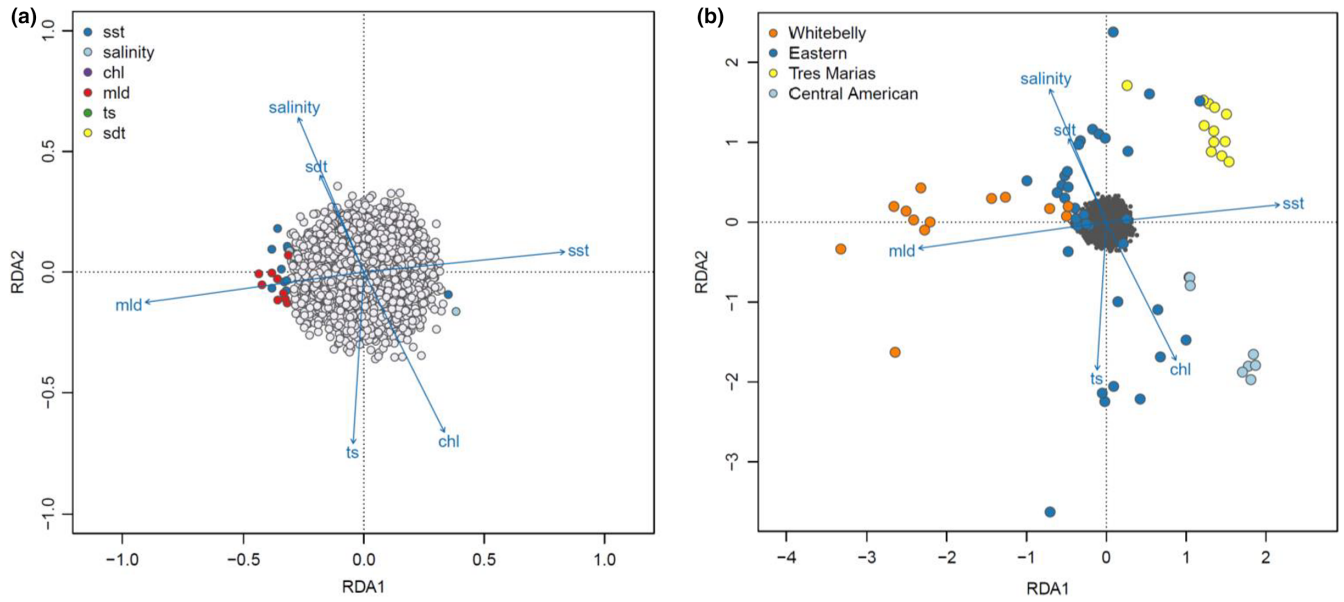

FIGURE 3 Redundancy analysis (RDA) axes 1 and 2 conducted using 8994 SNPs, plotted with symmetrical scaling. Environmental variables are indicated by blue vectors. (a) Outlier SNPs from RDA axis 1 are highlighted in colour based on the environmental variable with the strongest correlation, and all other SNPs are light grey. (b) Individual dolphins are highlighted in colour based on ecotype, and SNPs are dark grey. sst = sea surface temperature, salinity = surface salinity, chl = chlorophyll concentration, mld = mixed layer depth, td = thermocline depth, ts = thermocline strength, sdt = standard deviation of temperature from 0 to 300 m [Colour figure can be viewed at wileyonlinelibrary.com]

are probably interacting with the multivariate environment. This idea was supported by visualization of the loadings for the outlier SNPs on the RDA axes (Figure 3a).

The first RDA axis also correlated strongly with individual ecotypes, separating the ecotypes into three groups: whitebelly, eastern and the two coastal ecotypes (Central American and Tres Marias; Figure 3b). The coastal ecotypes occupy the warmest waters with the shallowest mixed layer, and the whitebelly occupies the coldest waters with the deepest mixed layer. Although the second RDA axis was not significant, this axis reveals habitat differences between the two coastal ecotypes, with the Tres Marias ecotype occupying habitats with higher salinity, a weaker thermocline and lower chlorophyll concentration than the Central American ecotype.

Population genetic structure outlier tests resulted in nine outlier SNPs for FDIST, two for OUTFLANK, and two for PCADAPT when using strict significance thresholds to account for multiple testing (q < 0.05 for OUTFLANK and PCADAPT; Bonferroni correction for FDIST). Both OUTFLANK outliers were also FDIST outliers, but the PCADAPT outliers were not shared with the F_{ST} outliers defined by FDIST and OUTFLANK. We also investigated outlier SNPs identified with a lower stringency significance threshold, since population structure outlier tests can have low power due to a variety of factors, such as when selection acts on multiple loci that each contribute a weak effect on the phenotype (Forester et al., 2018). When using a lower stringency threshold of p < .05, the number of outlier SNPs was 753 for FDIST, including 645 divergent selection outliers and 108 balancing selection outliers; 250 outlier SNPs for OUTFLANK; and 537 outlier SNPs for PCADAPT (Tables S3–S6). There was strong overlap in the outliers for

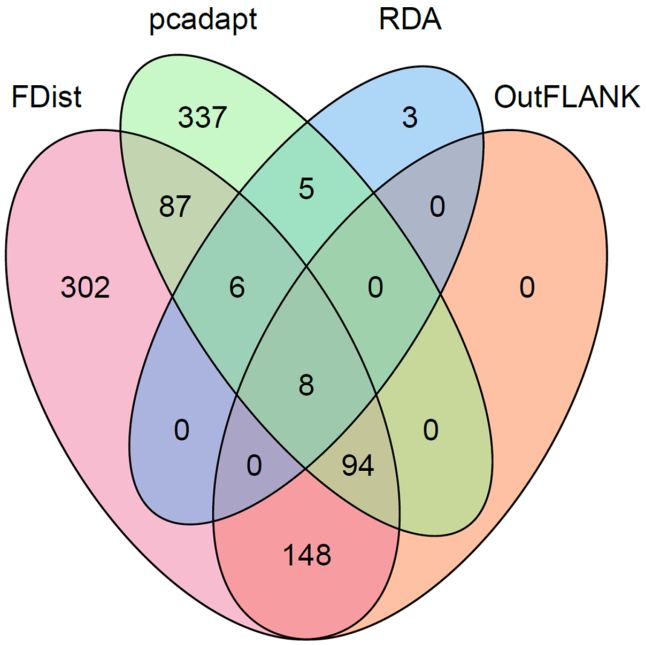

FIGURE 4 Venn diagram of 990 SNPs identified as outliers by FDIST, OUTFLANK, PCADAPT and RDA. For FDIST, only SNPs identified as putatively under divergent selection are reported [Colour figure can be viewed at wileyonlinelibrary.com]

the two F_{ST} outlier tests; all OUTFLANK outliers were also FDIST outliers for divergent selection (Figure 4). In addition, 36.3% of PCADAPT outliers were also F_{ST} outliers for divergent selection (195 out of 537 outliers), 63.6% of RDA outliers were both global F_{ST} outliers for divergent selection and PCADAPT outliers (14 out of 22 outliers), and an

additional 22.7% of RDA outliers were PCADAPT outliers but not F_{ST} outliers (five out of 22 outliers) (Figure 4).

PCA using only outlier SNPs from each of the divergent selection outlier tests (Figure 2b–d) and outliers from all of these tests combined (Figure 2f) separated the whitebelly and Central American ecotypes, whereas the eastern and Tres Marias ecotypes clustered together; this pattern was strongest for the divergent F_{ST} outliers (Figure 2d). As expected, the balancing selection F_{ST} outliers deviated from this pattern, showing no separation of ecotypes (Figure 2e). In addition, PCA with only nonoutlier (i.e., neutral) SNPs showed no separation of ecotypes (Figure 2g).

Pairwise F_{ST} values calculated using only the 645 SNPs identified as divergent selection F_{ST} outliers were substantially larger than those calculated using all SNPs (0.052–0.153, $p < .0001$ for all; Table S7). In contrast, pairwise F_{ST} values calculated using only nonoutlier SNPs (7863 SNPs after "thinning" the full set of nonoutlier SNPs) were nonsignificant for all ecotype pairs. Pairwise F_{ST} values calculated using only balancing selection SNPs were also nonsignificant for all ecotypes.

3.5 | Gene ontology enrichment tests

RDA outliers ($N = 22$ SNPs) were associated with (i.e., occurred within 0.1 Mb of) 19 genes. For the GO enrichment analysis of RDA outliers using all *Tursiops truncatus* genes as background, no GO terms were enriched. However, for GO enrichment analysis of RDA outliers conducted using only sampled genes as background, we found moderate evidence for an overrepresentation of genes involved in social behaviour (two genes; $p = .00056$, FDR = .20) and protein localization to the nucleus (two genes; $p = .00056$, FDR = 0.20; Table S8). One gene had both the social behaviour and protein localization GO terms (*Dvl1*), one gene had only the social behaviour GO term (*Shank*I), and one gene had only the protein localization GO term (*BMP7*). These three genes were among only 13 genes associated with outliers from all four tests for divergent selection.

F_{ST} outliers for divergent selection ($N = 645$ SNPs, FDIST and OUTFLANK, $p < 0.05$) were associated with 394 genes. For the GO enrichment analysis conducted using all sampled genes as background, the highest ranking GO term for these genes was blood vessel remodelling, but the FDR for this result was high ($p = 0.0015$, FDR = 0.68) and this GO term was not significantly enriched when using all *T. truncatus* genes as background (Table S9). However, a number of other biological processes were significantly enriched when using all *T. truncatus* genes as background, including regulation of nervous system development ($p = 1.6E{-}07$, FDR = 0.00014), which was also significantly enriched for analyses including both divergent and balancing selection F_{ST} outliers (see below) (Table S10).

When including both divergent selection and balancing selection F_{ST} outliers ($N = 753$ SNPs, FDIST and OUTFLANK, $p < 0.05$), GO enrichment analysis with all sampled genes as background found moderate evidence for overrepresentation of genes involved in hippocampus development ($p = .00037$, FDR = 0.16); five genes had this GO term: *Pafah1b1*, *Tsc1*, *BCAN*, *NF2* and *Cdk5* (Table S11). Three of these genes were associated with divergent selection, and two with balancing selection. For enrichment analysis using all *T. truncatus* genes as background, hippocampus development was moderately enriched ($p = .00054$, FDR = 0.059), and the related GO term of regulation of nervous system development was significantly enriched, with four of the five hippocampus development genes also associated with this GO term ($p = 7.1E{-}08$, FDR = 0.000068) (Table S12).

PCADAPT outliers ($N = 537$ SNPs, $p < 0.05$) were associated with 346 genes. When using all sampled genes as background, the highest ranking GO term was negative regulation of the canonical Wnt signalling pathway ($p = 0.0015$, FDR = .35); 10 genes had this GO term (Table S13). When using all *T. truncatus* genes as background, this GO term was also significantly enriched ($p = .000026$, FDR = .0086) (Table S14).

4 | DISCUSSION

We found evidence for local adaptation of spinner dolphins within the ETP using genome scans aimed at identifying outliers for genotype–environment associations and population differentiation (F_{ST} and PCA). These approaches found relatively strong overlap across methods in the outliers identified; the percentage of outlier SNPs shared with at least one other outlier test was 86.4% for the GEA test (conducted using RDA), 46.8% for F_{ST} outlier tests (calculated for FDIST and OUTFLANK, including only divergent selection outliers) and 37.2% for PCADAPT. This overlap suggests that the different outlier tests are probably identifying some of the same biological phenomena, despite the different statistical approaches used for each test. The GEA outliers were associated with mixed layer depth and sea surface temperature, indicating that these environmental parameters are drivers of selection, or are correlated with other parameters driving selection, such as mating system or prey distribution. Mixed layer depth was strongly correlated with thermocline depth, which is thought to influence the effort required for prey capture (Fiedler et al., 1998). Sea surface temperature, which was also strongly associated with GEA outliers, could also influence the types and quantity of prey available, potentially leading to local adaptation through divergent selective pressures for morphological, physiological or behavioural adaptations associated with prey capture or digestion. We also found that mixed layer depth and sea surface temperature were both strongly associated with ecotype, with the significant RDA axis separating the ecotypes into three groups based on habitat differences: (i) whitebelly, (ii) eastern and (iii) coastal ecotypes (Tres Marias/Central American). Since ecotype distribution is closely associated with the same environmental parameters that are associated with outlier SNPs, our GEA analysis cannot differentiate whether the association between the environmental variables and outlier SNPs is driven by the environmental variables themselves, or other variables associated with ecotype differences, such as morphology, mating system or unmeasured environmental variables.

GO enrichment tests for GEA and population structure outliers identified a large number of genes related to social behaviour and cognitive processes compared to other functions. GEA outliers had moderate evidence for enrichment of genes associated with social behaviour, including two genes: *Shank1* and *Dvl1*. These two genes were associated with outlier SNPs identified across all four outlier tests, potentially indicating a strong association of these genes with ecotype and habitat. *Shank1* is associated with social behaviour and communication in both mice and humans, and is related to autism spectrum disorder, which causes social deficits in humans (Sungur et al., 2018). *Dvl1* is associated with social hierarchy and cooperative behaviour in mice, and may also be associated with autism (Belinson et al., 2016; Lijam et al., 1997; Long et al., 2004). For F_{ST} outliers, the GO enrichment test found evidence for enrichment of genes associated with hippocampus development and regulation of nervous system development, including five genes: *Pafah1b1*, *Tsc1*, *BCAN*, *NF2* and *Cdk5*. Of these genes, three (*Pafah1b1*, *Tsc1* and *Cdk5*) are also associated with autism (Barnett & Bibb, 2011; Sudarov et al., 2013; Tsai et al., 2013). *Pafah1b1* and *Cdk5* are also associated with learning and memory (Barnett & Bibb, 2011; Paylor et al., 1999). Three of these genes (*Pafah1b1*, *BCAN*, *Cdk5*) were associated with divergent selection and two with balancing selection (*Tsc1*, *NF2*), potentially indicating a range of selective forces acting on social and cognitive behaviours in the ETP. For PCADAPT outliers, we found evidence for GO enrichment of negative regulation of the canonical Wnt signalling pathway, including 10 genes. The Wnt signalling pathway regulates neural development and is one of the functional pathways with strong genetic associations to autism (Bae & Hong, 2018; Krishnan et al., 2016; Kwan et al., 2016).

The high numbers of outlier-associated genes related to social behaviour provides evidence that social differences between ecotypes may be a divergent evolutionary force in the ETP. This idea is supported by previous evidence for differences between these ecotypes in mating system and social behaviour. Morphological evidence indicates that all ETP ecotypes have a polygynous mating system except the whitebelly, which has a polygynandrous mating system (Perrin & Mesnick, 2003). The polygynous ecotypes (eastern, Tres Marias, Central American) have strong sexual dimorphism, high variation in male testis size, and strong correlation between male-specific morphological traits and testis size, indicating that some males dominate breeding and some males do not breed at all (Heske & Ostfeld, 1990; Perrin & Mesnick, 2003). For this type of mating system, sexual selection is expected to affect social behaviour by promoting premating competition among males for access to females, and the formation of social hierarchies for males (Emlen & Oring, 1977). In addition, polygynous mating systems often have more stable relationships among females (Rubenstein, 1986, 1994). In contrast, the whitebelly ecotype has little sexual dimorphism, low variation in testis size, and larger mean and maximum testis size compared to the eastern ecotype, indicating that sperm competition or postmating competition are more important than premating competition for this ecotype (Heske & Ostfeld, 1990; Perrin & Mesnick, 2003). As described above, these differences in mating system are thought to be a product of habitat differences; in particular, the high productivity and low thermocline depth in the eastern ETP may increase prey accessibility for the eastern/Tres Marias/Central American ecotypes, thereby increasing the availability of energy for reproductive competition among males and enabling a polygynous mating system (Perrin & Mesnick, 2003). Similar associations between resource availability and mating system have been observed in other species (Clutton-Brock, 1989; Emlen & Oring, 1977); for example, wild horses have been shown to exhibit a haremic mating system in resource-rich areas, but a fission–fusion system (i.e., weak group stability) in patchy habitats (Rubenstein, 1986).

A prior study also found evidence for a genomic signature potentially related to mating system differences for spinner dolphins in the ETP and across the IndoPacific (Andrews et al., 2013). This study found much stronger divergence at the Y chromosome than other markers for the most morphologically divergent spinner dolphin ecotypes across the IndoPacific (i.e., the ETP ecotypes compared to the dwarf ecotype, which occurs in southeast Asia and northern Australia, and the Gray's ecotype, which occurs across the rest of the tropical and subtropical IndoPacific), and proposed that this result was driven by restrictions in gene flow between ecotypes due to sexual selection involving male-specific characters. Although that study did not find significant Y chromosome divergence within the ETP, the F_{ST} values between the whitebelly and other ETP ecotypes were much higher for the Y chromosome than other markers (ranging from 0.107 to 0.183), and the lack of significance could be a result of low male sample sizes (Andrews et al., 2013).

Relatively little information is available regarding potential additional social behaviour differences between ETP ecotypes. However, visual aerial surveys indicate that the coastal ecotypes have more cohesive and larger groups than pelagic ecotypes, potentially indicating greater levels of social affiliation (Chivers et al., 2019; Perryman & Westlake, 1998). In addition, coastal ecotypes calve later in the year than pelagic ecotypes, indicating either that mating occurs later in the year or that gestation periods are longer (Chivers et al., 2019). Simultaneous multibeam echosounder observation of spinner dolphins and their prey in the Hawaiian Archipelago indicates that spinner dolphins use cooperative foraging behaviour (Benoit-Bird & Au, 2009), and variation in prey availability in the ETP could potentially lead to variation in the level and type of cooperative behaviour required for foraging. Furthermore, social behaviour is known to vary widely both within and across cetacean species (Andrews, 2014; Brakes & Dall, 2016; Hoelzel, 1998), and therefore variation in social behaviour across ETP ecotypes is highly plausible.

Studies of other species have also found associations between mating system and genes affecting social behaviour, learning and memory, and neural development. For example, many gene-targeted studies have found associations between vertebrate mating systems and arginine vasopressin and oxytocin (and the nonmammalian vertebrate homologues); these genes influence social affiliation by affecting pair bonding and parental care (Bendesky et al., 2017; Fischer et al., 2019; Oldfield et al., 2015). Studies comparing neural transcriptomes of closely related species with different mating systems have found

surprising evolutionary convergence in gene expression profiles associated with independent transitions from polygamy to monogamy across a wide taxonomic range of vertebrates, providing evidence for a universal toolkit of genes involved in the evolution of mating systems (Renn et al., 2018; Young et al., 2019). One of these studies examined a particularly broad taxonomic range and found evidence for consistent associations between mating system (monogamy vs nonmonogamy) and genes associated with neural development, synaptic activity, learning and memory, cognitive function, and other processes (Young et al., 2019). Another study comparing whole genome sequences of halictid bees from populations within a single species that had different mating systems (solitary vs group reproduction) found an association between mating system and a gene implicated in human autism (*syntaxin 1a*; Kocher et al., 2018).

In addition to the outlier-associated genes that showed evidence for functional enrichment in our study, many additional outlier-associated genes had functions that could be of interest based on our knowledge of ETP spinner dolphin biology (Tables S10, S12 and S14). For example, 13 outlier-associated genes had functions related to spermatid development (e.g., spermatogenesis, flagellated sperm motility, male meiosis, sperm axoneme assembly), including one gene that was an outlier for all four divergent selection outlier tests (*SPO11*); these genes could be involved in mating system variation through an influence on sperm competition. Other outlier-associated genes of potential interest had functions including development and sensory perception of taste.

Future studies should continue to explore the evolutionary processes driving diversification for spinner dolphin ecotypes in the ETP. Although we found evidence that social behaviour may be a driving force for adaptive divergence in this study system, our study was also relatively limited by sample sizes and genome coverage, which could lead to reduced power or spurious associations, and would miss signatures of selection that occur in regions of the genome that were not surveyed. Therefore, the outlier SNPs and associated genes identified here should be considered candidates for future work aimed at fully understanding their potential involvement in adaptive processes in the ETP. Future studies could use a targeted sequencing approach for candidate genes; targeted sequencing approaches are more cost-effective than RADseq for larger sample sizes, and typically have more lenient requirements for quantity and quality of genomic DNA, which are often limiting factors for studies of wild populations (Andrews et al., 2018). In addition, whole genome sequencing, while substantially more expensive that RADseq approaches, would provide a more thorough assessment of genome-wide associations for spinner dolphins across the ETP.

4.1 | Neutral population structure

Population structure analyses using all SNPs indicated weak but significant genetic divergence between the ETP ecotypes, with the whitebelly ecotype showing the greatest divergence; these results are in accordance with previous studies (Andrews et al., 2013; Dizon et al., 1991; Galver, 2002; Leslie et al., 2019; Leslie & Morin, 2016). sNMF analysis did not identify genetic structure across the ETP, aside from moderate evidence for clustering of the whitebelly ecotype, but PCA clustered individuals by ecotype, and all pairwise F_{ST} values between ecotypes were low but significant (ranging from 0.0026 to 0.0104). The F_{ST} values calculated using all unlinked SNPs in this study are slightly lower than those calculated using the same GBS data by Leslie and Morin (2016), potentially resulting from our removal of two samples from the data set after identification of a replicate pair and a pair of close relatives in the data set. When excluding SNPs that were identified as outliers by one or more outlier analyses, none of the pairwise F_{ST} comparisons between ecotypes was significant, indicating that genetic divergence between ETP ecotypes is largely driven by the outlier SNPs. The weak but significant population genetic structure indicates the ETP is not panmictic, but that some gene flow probably occurs between ecotypes. Alternatively, barriers to gene flow between ecotypes could have been established recently enough that mutation–migration–drift equilibrium has not yet been achieved (Whitlock & McCauley, 1999).

Minimal population genetic structure across the ETP has been found for other cetacean species (e.g., Chen et al., 2018; Leslie & Morin, 2016; Van Cise et al., 2016) and pelagic fishes (e.g., Cardeñosa et al., 2014; Mamoozadeh et al., 2020). For the spotted dolphin, which has a similar distribution as spinner dolphins in the ETP and sometimes schools together with this species, GBS data (3721 SNPs) identified weak but significant genetic divergence between two offshore ETP populations (F_{ST} = 0.0019), and moderate divergence between the offshore populations vs a coastal population (F_{ST} = 0.0416 and 0.0734) (Leslie & Morin, 2016). In contrast, prior studies using mitochondrial sequences and seven microsatellite loci did not detect significant genetic divergence between the two offshore spotted dolphin populations, suggesting a lack of statistical power compared to the GBS data (Escorza-Treviño et al., 2005; Leslie et al., 2019). Future studies using genome-wide markers for additional species may uncover fine-scale population structure and adaptive genomic variation within the ETP.

4.2 | Management implications

Knowledge about adaptive genomic variation has potential to benefit multiple areas of conservation decision-making, such as the designation and prioritization of management units, assessment of vulnerability to environmental change, and choosing source populations and recipient sites for assisted gene flow (Allendorf et al., 2010; Funk et al., 2012, 2019; Hoelzel et al., 2019; McMahon et al., 2014). Although the practical aspects of incorporating adaptive genomic information into management decision-making are complicated and currently the subject of discussion and debate (Hoelzel et al., 2019; Mable, 2019; Shafer et al., 2015; Xuereb et al., 2020), managers have already begun using this type of information and will probably use it with increasing frequency in the future (Funk et al., 2019).

Evidence for adaptive divergence between ETP spinner dolphin ecotypes could assist in conservation decision-making. Hundreds of thousands of spinner dolphins died as bycatch in the yellowfin tuna

purse-seine fishery in the 1960s and early 1970s prior to the implementation of fishery regulations after the passage of the Marine Mammal Protection Act of 1972 (Wade, 1995). By 1980, dolphin bycatch had been reduced by 95% for US tuna fishing vessels, but the last census of ETP spinner dolphins in 2006 indicated that these dolphins had failed to recover from depletion (Wade et al., 2007). Currently these dolphins are managed as three stocks (whitebelly, eastern/Tres Marias, Central American) based on morphological, population genetic and behavioural differences. Arguments have also been made that the Tres Marias ecotype should be designated as a separate stock from the eastern ecotype due to genetic distinctiveness (Leslie & Morin, 2016).

Our evidence for adaptive genomic differences between ETP ecotypes bolsters support for stock designations, indicating that managing stocks separately could help preserve adaptive genomic variation and behavioural differences, as well as increase capacity for responding to environmental change (Funk et al., 2012). RDA indicated that adaptive genomic variation is stratified most strongly from west to east within the ETP (i.e., the first axis in Figure 3b; the second axis was nonsignificant), and this result was supported by population structure analyses based on outlier SNPs, which found strong separation of the whitebelly and Central American ecotypes (Figure 2). The Tres Marias ecotype clustered together with the eastern ecotype in the outlier PCAs, but clustered separately from the eastern ecotype on the first RDA axis, potentially indicating weak but significant adaptive divergence between the Tres Marias and eastern ecotypes.

Our results suggest that climate change may impose strong shifts in adaptive pressures on ETP ecotypes, given that the environmental variables most closely associated with adaptive genomic variation for these ecotypes (i.e., thermocline depth and sea surface temperature) are expected to be heavily impacted by ocean warming in the ETP (Fiedler & Lavin, 2017). Studies have shown deeper thermocline, higher sea surface temperature and reduced biological productivity in warm El Niño periods (Fiedler, 2002; Fiedler & Lavin, 2017) and warm phases of the Pacific Decadal Oscillation (El Viejo) periods (Pennington et al., 2006), possibly offering a prediction of the physical–biological impacts of rising ocean temperatures in this region. For ETP spinner dolphins, life history strategies that evolved in step with a suite of oceanographic features may be disadvantageous in a restructured ocean with altered periodic perturbations. However, our evidence for a genomic basis to phenotypic differences suggests that ETP ecotypes have "adaptive potential" for evolving in response to climate change (Funk et al., 2019). The large population sizes and presumably high gene flow across the ETP could also contribute to adaptive potential. Nevertheless, the evolutionary responses could also be impeded by the complexity of optimal phenotypes in the ETP; optimal phenotypes in this region are probably defined by multiple interacting morphological and behavioural traits. In addition, interactions between physical environmental change (ocean warming) and human interventions (fisheries bycatch) must be considered in management decisions designed to maintain adaptive potential (Fiedler, 2002). Modelling approaches that incorporate adaptive genomic variation could help evaluate the adaptive potential of spinner dolphins to respond to climate change in the ETP (Funk et al., 2019).

5 | CONCLUSIONS

Genome scans using outlier tests for population differentiation and GEAs revealed evidence for putative local adaptation at the genomic level for spinner dolphin ecotypes within the ETP. Outlier SNPs were associated with a large number of genes related to social behaviour, providing potential evidence for local adaptation driven by selective pressures on behaviour. This idea is supported by previous studies identifying different mating systems between ecotypes. Our results provide evidence that divergent selection on genes associated with social behaviour may be a strong evolutionary force for spinner dolphins in the ETP despite probable ongoing gene flow and no differentiation at the subset of 7863 loci identified as neutral.

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AUTHOR CONTRIBUTIONS

KRA, ARH, PAM and MSL designed the study. MSL organized and prepared samples for library preparation. KRA and BE conducted genomic analyses. KRA led the writing of the paper, and all authors contributed to the writing.

DATA AVAILABILITY STATEMENT

The raw GBS sequence reads are available at the NCBI Short Read Archive (Bioproject accession no. PRJNA687544). Sampling locations and environmental data are available in Table S1. Benefits from this study include the sharing of these data on NCBI.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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